

Variance in prey abundance influences time budgets of breeding seabirds: evidence from pigeon guillemots *Cepphus columba*

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We use data on pigeon guillemots *Cepphus columba* to test the hypothesis that discretionary time in breeding seabirds is correlated with variance in prey abundance. We measured the amount of time that guillemots spent at the colony before delivering fish to chicks (“resting time”) in relation to fish abundance as measured by beach seines and bottom trawls. Radio telemetry showed that resting time was inversely correlated with time spent diving for fish during foraging trips ($r = -0.95$). Pigeon guillemots fed their chicks either Pacific sand lance *Ammodytes hexapterus*, a schooling midwater fish, which exhibited high interannual variance in abundance ($CV = 181\%$), or a variety of non-schooling demersal fishes, which were less variable in abundance (average $CV = 111\%$). Average resting times were 46% higher at colonies where schooling prey dominated the diet. Individuals at these colonies reduced resting times 32% during years of low food abundance, but did not reduce meal delivery rates. In contrast, individuals feeding on non-schooling fishes did not reduce resting times during low food years, but did reduce meal delivery rates by 27%. Interannual variance in resting times was greater for the schooling group than for the non-schooling group. We conclude from these differences that time allocation in pigeon guillemots is more flexible when variable schooling prey dominate diets. Resting times were also 27% lower for individuals feeding two-chick rather than one-chick broods. The combined effects of diet and brood size on adult time budgets may help to explain higher rates of brood reduction for pigeon guillemot chicks fed non-schooling fishes.

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Flexible time-activity budgets allow some animals to moderate the effects of declining food availability by spending more time foraging (Herbers 1981). Seabirds typically prey on animals that are highly ephemeral and patchy in their distribution, and might therefore be expected to have especially flexible time budgets that allow them to greatly increase the amount of time spent foraging when food availability declines. This prediction has been supported by studies of a wide variety of seabird species that have shown that as food supply declines birds spend less time at the colony and more time at sea foraging (Montevicchi 1993, Furness 1996, Monaghan 1996). This flexible time allocation is recognized as an important adaptation for buffering seabird breeding success against variability in food supply, and

it has often been suggested that adult time budgets might serve as sensitive monitors of the population status of seabird prey (Cairns 1987a, Montevicchi 1993, Furness 1996).

However, the ability to buffer against declining food abundance with flexible foraging effort varies widely among species. Some species, such as the common murre *Uria aalge* are able to buffer chick growth rates and reproductive success against large (9- to 40-fold) interannual changes in food abundance (Burger and Piatt 1990, Monaghan et al. 1994, Uttley et al. 1994, Zador and Piatt 1999). Other species, such as Arctic terns *Sterna paradisaea* and black-legged kittiwakes *Rissa tridactyla* fail to breed entirely in the face of similar declines in food abundance, in spite of increas-

ing foraging effort (Monaghan et al. 1992, Hamer et al. 1993). Accepted explanations for these inter-specific differences in buffering ability typically have to do with intrinsic features of seabird biology. These include body size (Pearson 1968, Furness 1996), foraging mode (Monaghan et al. 1996, Caldow and Furness 2000), the amount of time that must be allocated to other activities, such as nest defense (Hamer et al. 1991, 1993), and life-history traits, such as clutch size (Stearns 1992, Ratcliffe and Furness 1999).

Less is known about extrinsic factors, such as characteristics of prey species, that may also affect flexibility in time-activity allocation. One such extrinsic factor is the amount of variability in abundance in different prey populations. Sutherland and Moss (1984) proposed that the amount of discretionary time available to an animal should be positively correlated with variance in prey encounter rates. This "prey variance" hypothesis is consistent with foraging theory that predicts that animals exploiting clumped or ephemeral prey such as schooling fish need to invest less time in foraging activities than animals feeding on solitary prey (Perry and Pianka 1997). Piscivorous seabirds are excellent subjects for tests of the prey variance hypothesis because they eat both schooling midwater fishes and solitary demersal fishes, and spatial-temporal variance in abundance is probably greater for schooling than non-schooling fishes (Bradstreet and Brown 1985, Cairns 1987b). The prey variance hypothesis therefore predicts that flexibility in time allocation should increase with the proportion of schooling fishes in the diet.

In this paper we use data on pigeon guillemots *Cephus columba* to test the hypothesis that flexible time allocation in breeding seabirds is a function of predation on variable schooling prey. Pigeon guillemots are an attractive study species because they have the most diverse diet of any auk (Ewins 1993). Birds at some colonies feed their chicks non-schooling demersal fishes almost exclusively, while the diet at other colonies consists mostly of schooling midwater fishes. Comparisons of time budgets may therefore be made between groups of pigeon guillemots with different diets, and such intraspecific comparisons allow confounding intrinsic variables such as body size and life history traits to be controlled. We used a measure of discretionary time spent at the colony ("resting time") to test three predictions of the prey variance hypothesis. Compared to pigeon guillemots feeding on non-schooling prey, we predicted that pigeon guillemots feeding on schooling prey would have: (1) higher mean resting times, (2) more variable resting times, and (3) would be better able to use flexible time allocation to buffer meal delivery rates against declines in prey abundance. We used measures of fish abundance from bottom trawls and beach seines to characterize prey availability during the study, as well as to compare variability between schooling and non-schooling prey species.

Cephus guillemots commonly raise two chicks to 80–100% of adult mass in the nest, and this represents a higher parental investment in nest-bound chicks than is made by any other any auk (Sealy 1973, Ydenberg 1989). Average brood size for successful nests in the present study was 1.61 chicks, and average fledging mass was 93% of average adult mass (Litzow et al. 2002). This high reproductive commitment might be expected to reduce flexibility in time allocation if parents are typically working at a high proportion of maximal effort. However, although much research has centered on the role of nestling demand in determining provisioning rates, less research has focused on the relationship between nestling demand and utilization of discretionary time by adults (see Ratcliffe and Furness 1999). We therefore also examined the effect of natural variability in brood size on parental time budgets.

Methods

Study area

We collected data in Kachemak Bay (59° 35' N, 151° 19' W), which is located on the east shore of lower Cook Inlet, Alaska. Pigeon guillemots are semi-colonial, and in Kachemak Bay they nest in approximately 30 loose colonies of 2–15 nests each and in numerous solitary sites. Approximately 500–600 adults are present in the area during the breeding season (unpubl. data).

Kachemak Bay is bisected into oceanographically distinct inner and outer sections by the Homer Spit (Fig. 1). The Outer Bay is dominated by input from the Gulf of Alaska and is well mixed and relatively cold and saline, while the Inner Bay is influenced by river runoff and tends to be more stratified, warmer, and less saline (Abookire et al. 2000). During summer in 1996–1998 median monthly surface temperatures averaged 0.9°C higher, and median monthly surface salinity aver-

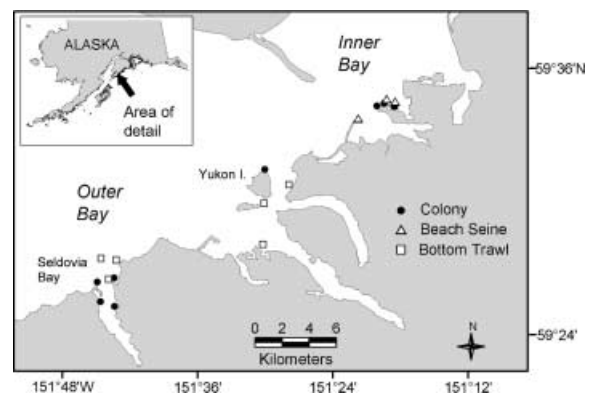


Fig. 1. Location of pigeon guillemot study colonies, beach seine sites and bottom trawl sites in Kachemak Bay, Alaska.

aged 3.1 PSU lower, in the Inner Bay (Abookire et al. 2000). These differences in oceanography have important implications for breeding pigeon guillemots. A midwater schooling fish, the Pacific sand lance *Ammodytes hexapterus*, is about 50% more abundant, on average, in the Inner Bay, and spatial and interannual variability in sand lance abundance is correlated with variable oceanography (Abookire et al. 2000, Litzow et al. 2002). Sand lance may also be more abundant around Inner Bay colonies because they are surrounded by extensive shallow, sandy seafloors that provide excellent sand lance habitat (M.L., pers. obs.). During this study pigeon guillemots in the Inner Bay fed their chicks mostly sand lance (59% of meals) and switched to demersal fishes when sand lance abundance declined, while pigeon guillemots nesting in the Outer Bay fed their chicks non-schooling fishes almost entirely (94% of meals), and did not switch to sand lance when demersal fish abundance declined (Litzow et al. 2000, 2002). The primary prey species in the Outer Bay were gunnels (Pholidae), pricklebacks *Lumpenus* spp., sculpins (Cottidae) and flatfish (Pleuronectidae). In this paper we treat the Inner and Outer Bay as independent foraging areas. This decision is justified by the pervasive diet differences noted above, by the fact that most colonies in the two areas are separated by more than 20 km, twice the maximum reported foraging range of the species (Ewins 1993), and by the observation that radio-tagged individuals forage only in the area they nest in (unpubl. data). We use area as a proxy for diet, with individuals from the Inner Bay as a "schooling fish diet" group and those in the Outer Bay as a "non-schooling diet" group.

Data collection

Colony-based studies of seabird time budgets typically use the amount of time that adults spend at the nest site as inverse measures of time spent away from the colony foraging (e.g., Pearson 1968, Burger and Piatt 1990, Caldow and Furness 2000). Such measurements are not possible for pigeon guillemots, which are cavity nesters that typically do not attend the nest after chicks are c. 5–7 days old (Ewins 1993). Instead we measured "resting time", or the amount of time that adults spent on the water in front of the colony, as pigeon guillemots typically remain on the water in front of the colony with a fish for as long as an hour before delivering to the nest. While we use the term "resting time" for convenience, we recognize that this measure represents discretionary time that could be used in a variety of activities, such as predator detection and social interaction (Herbers 1981).

We collected time budget data in July and August during 1996–1998 at five colonies in two areas of the

Outer Bay (Yukon I. and Seldovia Bay, Fig. 1) and during 1996–1999 at three neighboring colonies in the Inner Bay. Average breeding success during the study was low (0.38 chicks fledged nest⁻¹, Litzow et al. 2002), with many instances of egg predation, and as a result no individual colony was active for every year of the study. We observed breeding pigeon guillemots from anchored boats (using binoculars) or from blinds (using telescopes) during all-day watches (06:00–22:00). We watched two to five nests during each watch, and typically could not identify individual mates, so we use the nest as our sample unit. Each nest was watched one to three times per year, and unless repeated-measures analysis was used, data from multiple watches of a single nest in one year were averaged before analysis. For each meal delivery we recorded the time that the adult arrived on the water in front of the colony and the time that it delivered the meal. We define resting time as the amount of time that a bird remained on the water with a fish before delivering to the nest. Throughout this paper we refer to "delivery rate" (meals h⁻¹) to distinguish our data from "provisioning rate" (g h⁻¹ or kJ h⁻¹, Emms and Verbeek 1991).

We confirmed the relationship between resting time and foraging time budgets by following radio-tagged birds in 1999 (n = 6). In each study area we caught three adults that were provisioning chicks and attached radios to four central tail feathers with glue and cable ties. Radios weighed 3.5–4.0 g (<1% of body mass), and we assessed radio effects by comparing the delivery rate of three tagged birds with their non-tagged mates during all-day watches. We followed radio-tagged birds with a 7.6 m boat and recorded time at the colony holding fish (the "resting time" measurement that we made during provisioning watches) and the proportion of time spent in three behavioral categories while birds were away from the colony on foraging trips: time on the surface of the water, time diving, and time flying. We waited at least 24 hours after capture before observing tagged birds, and we followed individual birds for 6.5–10.7 hours.

We measured sand lance abundance with beach seines and demersal fish abundance with bottom trawls (detailed methods in Abookire et al. 2000, Litzow et al. 2000). These earlier papers report data from beach seines and bottom trawls that were set in both areas of Kachemak Bay. However, in the present study we were interested in relating pigeon guillemot behavior to the abundance of primary prey for particular colonies during the period when behavioral observations were made. This paper therefore only uses beach seine data from the Inner Bay (sand lance diet area) and bottom trawl data from the Outer Bay (demersal diet area). We further restricted the fish data that we used in this study to achieve spatial and tem-

poral overlap with our pigeon guillemot behavioral data. There are therefore some differences between the results of this paper and earlier papers (Litzow et al. 2000, 2002) that drew on a larger set of fish data. Sand lance abundance was measured with beach seine catch per unit effort (CPUE; fish set⁻¹) at three sites around Inner Bay colonies every two weeks during the period when time budget data were collected (1 July–12 August, *n* = 68 sets). Demersal fish abundance was measured with bottom trawl CPUE (fish 1000 m⁻²) at four to six sites made once a year during mid August (*n* = 16 sets). Sampling schooling fish repeatedly allowed us to relate resting times from individual all-day watches in the Inner Bay (schooling diet) to the abundance of sand lance from seines set within one week of those watches. Because bottom trawl stations were only sampled once each summer, we only make annual-scale comparisons for pigeon guillemots feeding on non-schooling fishes.

Statistical analysis

Because our sampling effort was limited to four years in the Inner Bay and three years in the Outer Bay, we did not have adequate statistical power for regression analysis of the relationship between time budgets and food abundance. Instead we used a categorical approach, classifying each year as “high” or “low” abundance for each prey type. Multiple beach seines made at a single site violate assumptions of independence, so we treated individual sets as subsamples nested within site factors in ANOVA (Zar 1999). In order to compare variability in sand lance and demersal fish abundance we calculated the coefficient of variability (CV) of annual mean CPUE values. CV for demersal species was averaged between Yukon I. and Seldovia Bay in order to control for spatial variability. We analyzed correlated response variables with MANOVA to assess overall effects followed by univariate ANOVA using type III sums of squares in PROC GLM, SAS (SAS Institute 2000). We calculated least-square means to compare effects of categorical explanatory variables. We made multiple observations of individual nests in the Inner Bay to examine the effects of seasonal changes in prey abundance on time budgets. We used repeated-measures methods to analyze these data, including nest identity (nested within brood size) as an explanatory variable to account for differences among breeding pairs. We used one-tailed tests for radio effects, since we hypothesized negative radio effects on provisioning behavior. We also used one-tailed tests for predictions of the prey variance hypothesis, since those predictions were directional. All prey abundance data were log (*x* + 1) transformed to correct for heteroscedasticity and proportional data were arcsine transformed to satisfy assumptions of normality. We present all means ± SE, and set $\alpha = 0.05$.

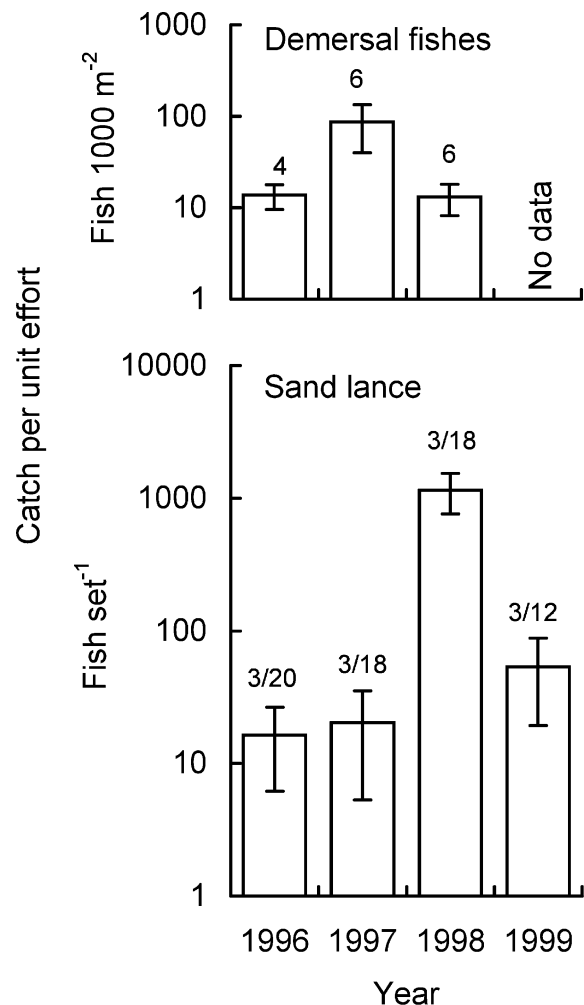


Fig. 2. Abundance of primary prey of pigeon guillemots in two study areas: demersal fishes in Outer Kachemak Bay and sand lance in Inner Kachemak Bay. Note log scales and different units on y-axes. Demersal fish data from 1999 are excluded because no behavioral data were collected in the Outer Bay that year. Demersal fish abundance was measured with bottom trawls, sand lance abundance was measured with beach seines. Sample sizes are number of sites for demersal fish, and number of sites/number of sets for sand lance. Error bars ± 1 SE.

Results

We measured 1693 resting times during 489 h of observing 65 nests (32 nests in the schooling fish group and 33 in the non-schooling fish group). Chicks in 37 of these nests were accessible so that we could determine brood size and chick age (20 in the schooling group, 17 in the non-schooling group).

Prey abundance

CPUE of demersal fishes around “non-schooling diet” colonies varied approximately 7-fold among years

(ANOVA, $F_{3,13} = 4.24$, $R^2 = 0.40$, $P = 0.04$; Fig. 2). We did not detect significant pairwise differences among years (Newman-Keuls test, $P > 0.05$). However, CPUE was more than six times greater in 1997 (87 ± 47 fish 1000 m^{-2}) than in either 1996 (14 ± 4 fish 1000 m^{-2}) or 1998 (13 ± 5 fish 1000 m^{-2}). We therefore classified 1997 as a “high demersal” year and 1996 and 1998 as “low demersal” years. This classification is justified by patterns of brood reduction, which was three times more common in the Outer Bay during “low” demersal years than during the “high” demersal year (Litzow et al. 2002).

Sand lance CPUE around “schooling diet” colonies varied 70-fold among years (nested ANOVA, $F_{3,36} = 5.81$, $R^2 = 0.19$, $P = 0.002$; Fig. 2). CPUE was higher in 1998 than either 1996 or 1997 (Newman-Keuls test, $P < 0.05$). CPUE in 1999 did not significantly differ from other years (Newman-Keuls test, $P > 0.05$). However, extremely high variability among samples limited the power of our statistical comparison, and CPUE was 26 times greater in 1998 (1430 ± 799 fish set^{-1}) than 1999 (54 ± 14 fish set^{-1}). We therefore included 1999 in a “low sand lance” group with 1996 and 1997, and classified 1998 as a “high sand lance” year.

Interannual CV of sand lance abundance in the Inner Bay was greater than that of the seven most common taxa in Outer Bay bottom trawls (one-sample $t_6 = -3.98$, $P = 0.007$; Table 1).

Radio effects

Two radio-tagged birds delivered more meals than their non-tagged mates, while one tagged bird delivered fewer meals than its mate. We did not detect a negative effect of radios on delivery rate (tagged mean = 0.44 ± 0.03 meals h^{-1} ; non-tagged mean = 0.52 ± 0.22 meals h^{-1} ; paired $t_2 = 0.33$, $P = 0.61$), although we recognize the low statistical power of this comparison. No radio-tagged birds abandoned their nests.

Table 1. Interannual coefficient of variation (CV) of schooling (sand lance) and non-schooling prey of pigeon guillemots. Value for sand lance is from beach seines set at three sites in the Inner Bay, values for demersal fishes are from bottom trawl CV averaged between Yukon I. and Seldovia Bay in the Outer Bay.

Common name	Scientific name	CV (%)
Pacific sand lance	<i>Ammodytes hexapterus</i>	181
Rock sole*	<i>Lepidopsetta bilineata</i>	23
Northern ronquil	<i>Ronquilus jordani</i>	88
Yellowfin sole	<i>Pleuronectes asper</i>	126
Yellow Irish lord	<i>Hemilepidotus jordani</i>	157
Arctic shanny	<i>Stichaeus punctatus</i>	124
Great sculpin	<i>Myoxocephalus polyacanthocephalus</i>	98
Crescent gunnel	<i>Pholis laeta</i>	157

* Split into two species after our study was completed (*L. bilineata* and *L. polyxystra*, Orr and Matarese 2000).

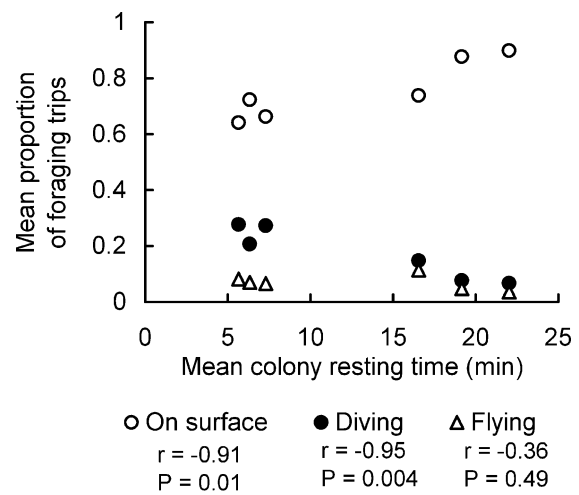


Fig. 3. Relationship between resting time at the colony and time-activity budgets during foraging trips for six radio-tagged pigeon guillemots. Statistics are from Pearson correlations with resting time.

Resting time as a measure of foraging effort

Resting time at the colony was a reliable indicator of time-activity budgets while away from the colony (Fig. 3). Radio-tagged birds with longer resting times at the colony spent less time diving while away from the colony (Pearson correlation; $r = -0.95$, $n = 6$ birds, $P = 0.004$), and more time on the surface of the water (Pearson correlation; $r = 0.91$, $n = 6$ birds, $P = 0.01$). We did not find a significant correlation between resting time and time spent flying (Pearson correlation; $r = -0.36$, $n = 6$ birds, $P = 0.49$), although we recognize the low statistical power of this analysis. Radio-tagged birds fell into two groups (Fig. 3), a group with higher resting times (two schooling diet birds and one non-schooling diet), and a group with lower resting times (one schooling diet and two non-schooling diet).

Predictions of the prey variance hypothesis

Prey type had a strong effect on time budgets. Average resting times were 46% higher at the Inner Bay (schooling diet) than at the Outer Bay (non-schooling diet). MANOVA showed that prey type had a significant overall effect on resting time and delivery rate (Wilks' $\Lambda_{2,60} = 0.86$, $P = 0.009$), and resting time was significantly affected by prey type and prey abundance ($F_{3,61} = 3.69$, $R^2 = 0.15$, $P = 0.02$; Table 2). Interannual variance in resting time was greater in the Inner Bay than in the Outer Bay (variance ratio test, $F_{3,2} = 25.95$, $P = 0.04$).

Pigeon guillemots feeding on schooling prey may have had more discretionary time because they tended to deliver fewer meals. Average delivery rates were 36% higher for the non-schooling prey group. Prey type and

Table 2. Resting times of pigeon guillemots in relation to prey type (schooling or non-schooling fish) and food abundance ("high" and "low" years): ANOVA results.

Term	df	MS	F	P
Prey type	1	604.3	9.50	0.003
Food abundance	1	268.1	4.21	0.04
Prey type \times Food abundance	1	107.1	1.68	0.20
Error	61	63.6		

prey abundance had a significant effect on delivery rates ($F_{3,61} = 2.76$, $R^2 = 0.12$, $P = 0.05$; Table 3). Pigeon guillemots with a majority schooling fish diet reduced resting times by 32% during years of low food abundance, but food abundance had no significant effect on delivery rates for this group (Fig. 4). In contrast, pigeon guillemots with a majority non-schooling diet were apparently unable to respond to decreased food supply with significant changes in time budgets, and delivery rates declined 27% during low-food years (Fig. 4). The difference in buffering ability was reflected by the significant effect of the prey type \times prey abundance interaction on delivery rates (Table 3). Differences in buffering ability were also illustrated by opposite signs of correlations between resting time and delivery rate for the two diet groups (Fig. 5). In the schooling group delivery rates increased when resting times declined (Pearson correlation of annual mean resting time and mean delivery rate; $r = -0.96$, $n = 4$ years, $P = 0.03$). In contrast, delivery rates decreased when resting times declined in the non-schooling diet group ($r = 0.99$, $n = 3$ years, $P = 0.048$).

We further examined this buffering ability by analyzing the effects of foraging ecology (proportion of schooling fish in the diet and schooling fish abundance) and chick demand (brood size and age) on resting times and delivery rates at known-content nests from the schooling prey group. This analysis included 20 nests that were each observed 1–3 times. Repeated-measures MANCOVA showed that prey abundance, chick age, the proportion of schooling fish in the diet and the prey abundance \times chick age interaction all had significant overall effects ($P \leq 0.04$). While we failed to detect a significant univariate effect on delivery rates ($F_{23,9} = 2.27$, $P = 0.10$), there was a significant effect on resting time ($F_{23,9} = 4.76$, $R^2 = 0.92$, $P = 0.01$; Table 4). Pigeon guillemots in the Inner Bay rested more when sand lance abundance was high (Fig. 6).

Table 3. Delivery rates of pigeon guillemots in relation to prey type (schooling or non-schooling fish) and food abundance ("high" and "low" years): ANOVA results.

Term	df	MS	F	P
Prey type	1	0.457	3.82	0.055
Food abundance	1	0.031	0.26	0.61
Prey type \times Food abundance	1	0.650	5.45	0.02
Error	61	0.119		

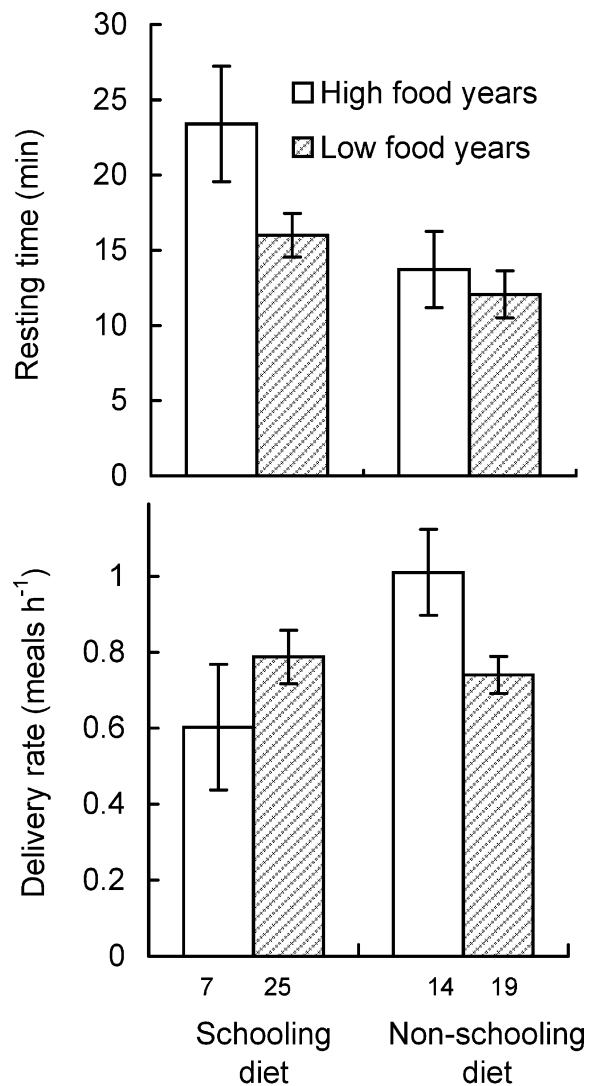


Fig. 4. Least-square means of pigeon guillemot resting times and delivery rates in relation to prey type and food abundance. Sample size (nests) given at base of columns, error bars ± 1 SE.

Brood size and time budgets

When prey type and chick age were accounted for, brood size had a significant overall effect on delivery rate and resting times (Wilks' $\Lambda_{2,30} = 0.68$, $P = 0.003$). Delivery rates were 71% higher when parents were feeding two-chick broods, and resting times were 27% lower (Fig. 7).

Discussion

This study supports the hypothesis that flexible time allocation in breeding seabirds is correlated with variance in prey abundance. Resting times were both higher

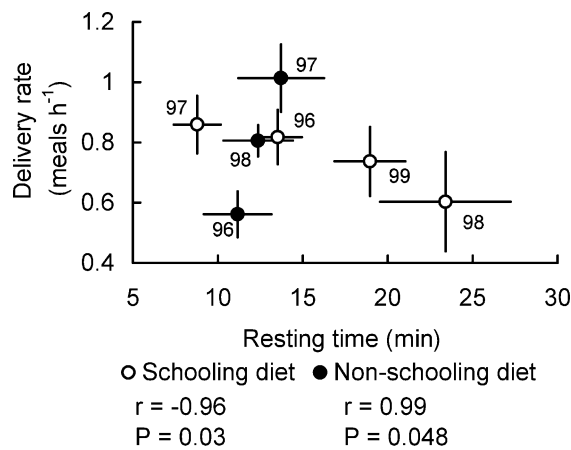


Fig. 5. The effect of diet on the relationship between time allocation and meal delivery rates in pigeon guillemots. Each dot represents average data from one diet group in a single year. Statistics are from Pearson correlations between resting time and delivery rate. Years are indicated next to dots, error bars ± 1 SE.

and more variable for the group of pigeon guillemots feeding mostly on schooling fish than for the group feeding mostly on non-schooling fish. These differences in time budgets reflected important differences in the foraging ecology of the two diet groups, as pigeon guillemots were able to use flexible time allocation to buffer meal delivery rates against declining food abundance only when schooling fish dominated the diet. The schooling fish diet group in this study also buffered against declining sand lance abundance by switching to demersal fishes. Our most comprehensive time series of diet data comes from one colony in the Inner Bay. Analysis of these data in conjunction with a more comprehensive set of beach seine data, including 1995 (when we did not collect time budget data), showed that the proportion of demersal fishes in diets increased from 15% during years of above-average sand lance abundance to 38% during years of below-average sand lance abundance (Litzow et al. 2002). However, this colony was not active during 1998, the year of “high” sand lance abundance in this study, so we did not analyze prey switching in concert with flexible time

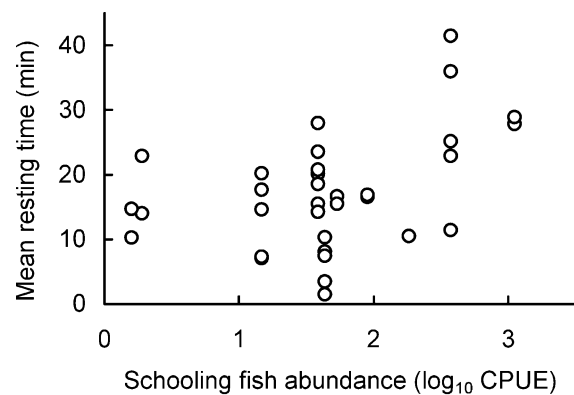


Fig. 6. Flexible time allocation by pigeon guillemots feeding on schooling fish: resting time in relation to fish abundance. Each point represents one nest-day. Fish abundance was measured with beach seines set within one week of behavioral watches. Repeated-measures ANCOVA demonstrated a significant relationship ($P = 0.006$).

allocation in this study. Understanding the relative importance of various behavioral buffering mechanisms remains a challenge in seabird ecology, and longer time series of diet composition and time budgets from individual *Cephus* colonies are needed to understand how these two buffering mechanisms work in concert.

Our results demonstrate the utility of colony resting time as a measure of foraging effort in pigeon guillemots. *Cephus* guillemots are the most neritic foragers among the piscivorous auks, and although demersal fishes typically dominate chick diets, midwater species are the majority items in diets in some areas (Ewins 1990, Golet et al. 2002), so time budgets of *Cephus* guillemots are potentially useful monitors of the availability of schooling prey in nearshore habitats (Prichard 1997, Litzow et al. 2000).

“Resting” time and foraging time-activity budgets

A key assumption of studies that use seabird colony attendance as an index of foraging effort is that birds spending less time at the colony spend more time foraging while away from the colony. Although our

Table 4. Resting times of pigeon guillemots in relation to foraging ecology (proportion of schooling fish in diet and schooling fish abundance) and nestling demand (brood size and chick age): repeated-measures ANCOVA results. Fish abundance was measured by beach seines set within one week of behavioral watches. This analysis only includes known-content nests from the area where schooling fish dominated the diet.

Term	df	MS	F	P
Brood size	1	173.8	8.12	0.02
Nest (brood size)	18	84.9	3.97	0.02
Chick age	1	230.2	10.76	0.01
Schooling fish abundance	1	276.6	12.93	0.006
Proportion schooling fish in diet	1	145.0	6.78	0.03
Fish abundance \times chick age	1	235.0	10.99	0.009
Error	9	21.4		

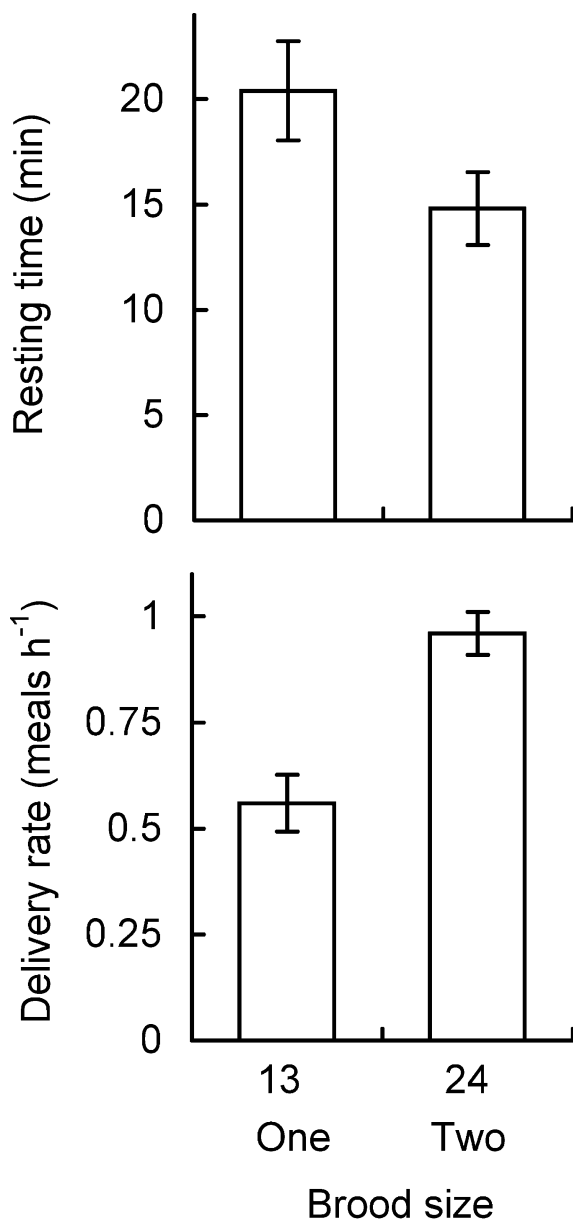


Fig. 7. The effect of brood size on pigeon guillemot delivery rate and parental resting time. MANCOVA demonstrated a significant overall effect ($P = 0.003$). Sample size (nests) given at base of columns, data are least-square means ± 1 SE.

sample of radio-tagged birds was small ($n = 6$), we found strong evidence that this assumption is valid for pigeon guillemots (Fig. 3). Individuals that rested longer at the colony spent less time diving and more time on the surface of the water than other birds. Previous studies have demonstrated similar relationships for other species. The amount of discretionary time spent at the nest-site is negatively correlated with the proportion of foraging trips spent underwater by common murres (Monaghan et al. 1994), and is also negatively correlated with foraging distance in northern

gannets *Morus bassanus* (Hamer et al. 2000). Within the schooling prey group resting time was more sensitive to variability in prey abundance than was meal delivery rate (Fig. 4), and is therefore superior as a parameter for monitoring schooling prey abundance.

Foraging ecology and flexible time allocation

We were able to observe both the schooling and non-schooling diet groups during one year of high abundance for their primary prey, and two to three years when prey were less abundant (Fig. 2). Average chick growth rates during the present study were 9% greater than the average value from five studies reviewed by Golet et al. (2000), suggesting that prey availability was relatively high during our study (Litzow et al. 2002). We cannot know if the number of years of "high" and "low" abundance for sand lance and demersal fish in this study was representative, as *Cephus* guillemots have not been previously studied in concert with schooling and non-schooling prey. However, variability in abundance was significantly greater for sand lance than for demersal fishes (Table 1). Although differences in variability in abundance between schooling and non-schooling fishes have been proposed as important features of seabird ecology (Bradstreet and Brown 1985, Cairns 1987b), we are not aware of other studies that have explicitly compared variability in abundance between the two prey groups.

Individuals in the Outer Bay (non-schooling prey) were apparently working near maximal capacity even during the year of high demersal fish abundance, and were unable to substantially increase foraging effort when food abundance declined (Fig. 4). This relationship between diet and discretionary time may also affect common murres, which had very little discretionary time at a colony with an anomalously high proportion of non-schooling demersal fishes in chick diets (Bryant et al. 1999). Comparisons within *Uria* also support the prey variance hypothesis. Thick-billed murres *U. lomvia* feed on a higher proportion of non-schooling fishes than common murres (Gaston and Jones 1998) and also typically spend less discretionary time at the nest-site (Falk et al. 2000).

Differences in average resting times between the two study areas might also be explained by average differences in food abundance. While demersal fish abundance is similar in the two areas, sand lance abundance is about 50% higher in the Inner Bay (Litzow et al. 2000), so pigeon guillemots in that area may simply have to expend less effort foraging because overall prey abundance is higher. However, both the lowest and highest annual average resting times were observed in the Inner Bay (Fig. 5), and interannual variance in resting times was greater in the Inner Bay than in the Outer Bay. This observation of increased flexibility is

consistent with the prediction that predation on highly variable prey will occasionally require greatly increased foraging effort in response to stochastic periods of prey scarcity (Sutherland and Moss 1984).

We found that prey type and prey abundance explained 12% and 15% of annual-scale variability in delivery rates and resting times, respectively. These are strong effects, considering that brood size and chick age were not accounted for in this analysis. When age and brood size were added to analysis of seasonal variability, we could account for 92% of variability in resting times of pigeon guillemots feeding on schooling fish (Table 4). This group made changes in time allocation in response to the proportion of sand lance in the diet and the availability of those fish (Table 4), and rested more when abundance was high (Fig. 6). However, identical sampling effort failed to find an effect on delivery rates, indicating that delivery rates were successfully buffered by flexible time allocation. This buffering ability is similar to that exhibited by common murre preying on sand lance (Monaghan et al. 1994, Uttley et al. 1994). The opposite signs of the correlations between resting time and delivery rate in the two diet groups give further evidence that the buffering effect of flexible time allocation was diet-dependant. Increased foraging effort (as shown by decreased resting times) was associated with higher delivery rates in the schooling diet group, but with lower delivery rates in the non-schooling group (Fig. 5).

Schooling and non-schooling prey in our study differed greatly in energy content, which is an important quality of prey for central place foragers (Drent and Daan 1980). The energy density (kJ g^{-1}) of Pacific sand lance is on average 1.7 times that of demersal pigeon guillemot prey (Van Pelt et al. 1997, Anthony et al. 2000), and diets rich in sand lance allow guillemots to deliver more energy to nestlings (Golet et al. 2000, Litzow et al. 2002). The higher energy density of schooling prey apparently helps pigeon guillemots with access to these prey to reduce meal delivery rates and increase resting times while maintaining high rates of energy flow to the nest.

The effect of different prey types on time budgets can also be understood within the context of foraging mode theory. "Widely foraging" predators typically feed on large or aggregated prey and are able to meet their energetic needs with less time spent foraging than "sit-and-wait" predators feeding on small or solitary prey (Perry and Pianka 1997). While we do not imply that predation on schooling fish necessarily forces pigeon guillemots to increase foraging range, the foraging mode dichotomy is relevant to time-activity allocation. For example, a sit-and-wait lacertid lizard *Eremias lineocellata* on average spends 43% of the day foraging, while a widely foraging congener *E. lugubris* spends only 11% of the day foraging (Nagy

et al. 1984). The time-intensive nature of predation on dispersed fish apparently means that pigeon guillemots typically have to spend a large proportion of the day foraging to meet energetic demands, and have little discretionary time to tap when food availability declines.

Brood size and time budgets

Finally, we found that natural variation in brood size drove differences in time budgets (Fig. 7). This finding was correlative, so we could not rule out other effects, such as differences in parental quality, that may have affected time budgets. However, brood manipulation experiments have also shown that changing nestling demand affects time-activity allocation in adult great skuas *Catharacta skua* (Ratcliffe and Furness 1999). Our correlative results may help explain diet-dependent patterns of brood reduction in pigeon guillemots. We found that the effort required to feed two-chick broods resulted in reduced parental resting time (Fig. 7), and that pigeon guillemots feeding on demersal prey had little discretionary time available (Fig. 4). Pigeon guillemots feeding on demersal prey experience brood reduction more frequently than those feeding on lipid-rich schooling prey, and brood reduction is more common for guillemots feeding on demersal prey when abundance of those prey declines (Golet et al. 2000, Litzow et al. 2002). This increase in brood reduction may result when individuals feeding on demersal prey are unable to feed two chicks without crossing some threshold of resting time below which adult body condition and survival are negatively affected. This interpretation is consistent with studies that have demonstrated that reproductive effort in seabirds reduces adult body condition and survival (Golet et al. 1998, Golet and Irons 1999), and with the tenet of life-history theory that long-lived animals such as seabirds should maximize expected lifetime reproductive success by limiting investment in any single reproductive event (Stearns 1992).

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References

- Abookire, A. A., Piatt, J. F. and Robards, M. D. 2000. Nearshore fish distributions in an Alaskan estuary in relation to stratification, temperature, and salinity. – *Estuar. Coast. Shelf Sci.* 51: 45–59.
- Anthony, J. A., Roby, D. D. and Turco, K. R. 2000. Lipid content and energy density of forage fishes from the northern Gulf of Alaska. – *J. Exp. Mar. Biol. Ecol.* 248: 53–78.
- Bradstreet, M. S. W. and Brown, R. G. B. 1985. Feeding ecology of the Atlantic Alcidae. – In: Nettleship, D. N. and Birkhead, T. R. (eds). *The Atlantic Alcidae*. Academic Press, London, pp. 263–318.
- Bryant, R., Jones, I. L. and Hipfner, J. M. 1999. Response to changes in prey availability by common murres and thick-billed murres at the Gannet Islands, Labrador. – *Can. J. Zool.* 77: 1278–1287.
- Burger, A. E. and Piatt, J. F. 1990. Flexible time budgets in breeding common murres: buffers against variable prey abundance. – *Stud. Avian Biol.* 14: 71–83.
- Cairns, D. K. 1987a. Seabirds as indicators of marine food supplies. – *Biol. Ocean.* 5: 261–271.
- Cairns, D. K. 1987b. The ecology and energetics of chick provisioning by black guillemots. – *Condor* 89: 627–635.
- Caldow, R. W. G. and Furness, R. W. 2000. The effect of food availability on the foraging behaviour of breeding great skuas *Catharacta skua* and arctic skuas *Stercorarius parasiticus*. – *J. Avian Biol.* 31: 367–375.
- Drent, R. H. and Daan, S. 1980. The prudent parent: energetic adjustments in avian breeding. – *Ardea* 68: 225–252.
- Emms, S. K. and Verbeek, N. A. M. 1991. Brood size food provisioning and chick growth in the pigeon guillemot *Cephus columba*. – *Condor* 93: 943–951.
- Ewins, P. J. 1990. The diet of black guillemots *Cephus grylle* in Shetland. – *Holarct. Ecol.* 13: 90–97.
- Ewins, P. J. 1993. Pigeon guillemot (*Cephus columba*). – In: Poole, A. and Gill, F. (eds). *The birds of North America*. The Academy of Natural Sciences and the American Ornithologists Union, Philadelphia, number 49, pp. 1–23.
- Falk, K., Benvenuti, S., Dall'antonia, L., Kampp, K. and Ribolini, A. 2000. Time allocation and foraging behaviour of chick-rearing Brünnich's guillemots *Uria lomvia* in high-arctic Greenland. – *Ibis* 142: 82–92.
- Furness, R. W. 1996. A review of seabird responses to natural or fisheries-induced changes in food supply. – In: Greenstreet, S. P. R. and Tasker, M. L. (eds). *Aquatic predators and their prey*. Fishing News Books, Cambridge, MA, pp. 166–173.
- Gaston, A. J. and Jones, I. L. 1998. *The Auks*. – Oxford University Press, Oxford.
- Golet, G. H., Kuletz, K. J., Roby, D. D. and Irons, D. B. 2000. Adult prey choice affects chick growth and reproductive success of pigeon guillemots. – *Auk* 117: 82–91.
- Golet, G. H. and Irons, D. B. 1999. Raising young reduces body condition and fat stores in black-legged kittiwakes. – *Oecologia* 120: 530–538.
- Golet, G. H., Irons, D. B. and Estes, J. A. 1998. Survival costs of chick rearing in black-legged kittiwakes. – *J. Anim. Ecol.* 67: 827–841.
- Golet, G. H., Seiser, P. E., McGuire, A. D., Roby, D. D., Fischer, J. B., Kuletz, K. J., Irons, D. B., Dean, T. A., Jewett, S. C. and Newman, S. H. 2002. Long-term direct and indirect effects of the Exxon Valdez oil spill on pigeon guillemots in Prince William Sound. – *Mar. Ecol. Prog. Ser.* 241: 287–304.
- Hamer, K. C., Furness, R. W. and Caldow, R. W. G. 1991. The effects of changes in food availability on the breeding ecology of great skuas *Catharacta skua* in Shetland. – *J. Zool. Lond.* 223: 175–188.
- Hamer, K. C., Monaghan, P., Uttley, J. D., Walton, P. and Burns, M. D. 1993. The influence of food supply on the breeding ecology of kittiwakes *Rissa tridactyla* in Shetland. – *Ibis* 135: 255–263.
- Hamer, K. C., Phillips, R. A., Wanless, S., Harris, M. P. and Wood, A. G. 2000. Foraging ranges, diets and feeding locations of gannets in the North Sea: evidence from satellite telemetry. – *Mar. Ecol. Prog. Ser.* 200: 257–264.
- Herbers, J. M. 1981. Time resources and laziness in animals. – *Oecologia* 49: 252–262.
- Litzow, M. A., Piatt, J. F., Abookire, A. A., Prichard, A. K. and Robards, M. D. 2000. Monitoring temporal and spatial variability in sandeel (*Ammodytes hexapterus*) abundance with pigeon guillemot (*Cephus columba*) diets. – *ICES J. Mar. Sci.* 57: 976–986.
- Litzow, M. A., Piatt, J. F., Prichard, A. K. and Roby, D. D. 2002. Response of pigeon guillemots to variable abundance of high-lipid and low-lipid prey. – *Oecologia* 132: 286–295.
- Monaghan, P. 1996. Relevance of the behaviour of seabirds to the conservation of marine environments. – *Oikos* 77: 227–237.
- Monaghan, P., Uttley, J. D. and Burns, M. D. 1992. Effects of changes in food availability on reproductive effort in arctic terns. – *Ardea* 80: 71–81.
- Monaghan, P., Walton, P., Wanless, S., Uttley, J. D. and Burns, M. D. 1994. Effects of prey abundance on the foraging behaviour, diving efficiency and time allocation of breeding guillemots *Uria aalge*. – *Ibis* 136: 214–222.
- Monaghan, P., Wright, P. J., Bailey, M. C., Uttley, J. D., Walton, P. and Burns, M. D. 1996. The influence of changes in food abundance on diving and surface-feeding seabirds. – *Can. Wildl. Serv. Occas. Pap.* 91: 10–19.
- Montevecchi, W. A. 1993. Birds as indicators of change in marine prey stocks. – In: Furness, R. W. and Greenwood, J. J. D. (eds). *Birds as monitors of environmental change*. Chapman and Hall, London, pp. 217–266.
- Nagy, K., Huey, R. and Bennett, A. 1984. Field energetics and foraging mode of Kalahari Lacertid lizards. – *Ecology* 65: 588–596.
- Orr, J. W. and Matarese, A. C. 2000. Revision of the genus *Lepidopsetta* Gill, 1862 (Teleostei: Pleuronectidae) based on larval and adult morphology, with a description of a new species from the North Pacific Ocean and the Bering Sea. – *Fish. Bull.* 98: 539–582.
- Pearson, T. H. 1968. The feeding biology of sea-birds on the Farne Islands, Northumberland. – *J. Anim. Ecol.* 37: 521–552.
- Perry, G. and Pianka, E. R. 1997. Animal foraging: past, present and future. – *Trends Ecol. Evol.* 12: 360–364.
- Prichard, A. K. 1997. Evaluation of pigeon guillemots as bioindicators of nearshore ecosystem health. – Unpubl. MS thesis, University of Alaska, Fairbanks.
- Ratcliffe, N. and Furness, R. W. 1999. The effect of parental age and experimentally manipulated brood size on the foraging effort and breeding performance of great skuas (*Catharacta skua*). – *J. Zool. Lond.* 249: 195–201.
- SAS 2000. *SAS/STAT User's Guide*, Version 8, 1st edn. – SAS Institute Inc., Cary, NC.
- Sealy, S. G. 1973. Adaptive significance of post-hatching developmental patterns and growth rates in the Alcidae. – *Ornis Scand.* 4: 113–121.
- Stearns, S. C. 1992. *The evolution of life histories*. – Oxford University Press, Oxford.
- Sutherland, W. J. and Moss, D. 1984. The inactivity of animals: influence of stochasticity and prey size. – *Behaviour* 92: 1–8.
- Uttley, J. D., Walton, P., Monaghan, P. and Austin, G. 1994. The effects of food abundance on breeding performance

- and adult time budgets of guillemots *Uria aalge*. – *Ibis* 136: 205–213.
- Van Pelt, T. I., Piatt, J. F., Lance, B. K. and Roby, D. D. 1997. Proximate composition and energy density of some North Pacific forage fishes. – *Comp. Biochem. Physiol.* 118A: 1393–1398.
- Ydenberg, R. 1989. Growth-mortality trade-offs and the evolution of juvenile life histories in the Alcidae. – *Ecology* 70: 1494–1506.
- Zador, S. and Piatt, J. F. 1999. Time-budgets of common murrelets at a declining and increasing colony in Alaska. – *Condor* 101: 149–152.
- Zar, J. H. 1999. *Biostatistical Analysis*, 4th ed. – Simon and Schuster, Upper Saddle River, NJ.

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